

SHORT COMMUNICATION

Courtship behavior and copulation in *Tengella radiata* (Araneae, Tengellidae)

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Abstract. The first description of the courtship behavior and copulation is provided for *Tengella radiata* (Kulczynski 1909). The male courts the female by rocking his body and vibrating his abdomen. These behaviors seem to induce the female to move out from her retreat onto the sheet and incline her body to facilitate intromission. The female has an active role during the courtship: strumming the tunnel and sheet threads, apparently inducing the male to increase the frequency and intensity of his courtship. Palpal insertion is extremely short. The female terminates the copulation by lunging at the male.

Keywords: Courting, sexual selection, funnel web spider

Tengella radiata (Kulczynski 1909) has a wide distribution in Costa Rica where it inhabits mature and secondary wet forests and coffee plantations from 50 to 1500 m elev. (Wolff 1977; Santana et al. 1990, pers. obs.), but it is, nevertheless, unknown outside of this small country. Its web consists of a large, horizontal sheet with an upper tangle that contains some cribellate threads and a tunnel at the “interior” section of the sheet (Santana et al. 1990; Eberhard et al. 1993; Eberhard & Pereira 1993). Spiders rest near the tunnel opening during the day.

The sexual biology of this spider is completely unknown. In nature males occasionally co-inhabit webs with adult females (W.G. Eberhard pers. comm), and I have occasionally observed males near or on the sheet of possibly adult females. Here I describe for the first time the courtship behavior and copulation of *T. radiata* and compare these behaviors to those of some species within families of the *Tengella*'s sister groups lycosoids and agelenoids (Coddington 2005). The family is of interest because it is a cribellate member of the Lycosoidea.

Courtship behavior and copulation of two pairs of *T. radiata* were filmed using a digital video camera Sony DCR-VX 1000 (30 frames/s). Both females were virgins raised from eggs in captivity and maintained in plastic boxes (30 × 18 × 11 cm) where they constructed their webs. One female was paired with one male that was also raised in captivity from different parents. The second female was paired with an adult male collected in the field. Male pre-copulatory and copulatory courtship behavior and copulation are defined as in Eberhard & Huber (1998). Male courtship refers to those behaviors that induce the female to respond in a way that favors the male's reproduction (Eberhard 1996). Copulation consists of all genitalic contact between a particular male-female pair, including the insertion of the embolus into the epigynal opening. It finishes when the pair separates from the copulatory position. Drawings were traced from video images. Spiders and egg sacs were collected near San Jose, Costa Rica; voucher specimens were deposited at the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica.

The first reaction of the male when placed on the female's web was to walk on the sheet, more or less randomly at first and then toward the tunnel opening where the female rested. Following this movement, courtship and copulation can be roughly divided into three consecutive phases seen in both pairs: courtship by male, while the female is in the tunnel, with the result that the female moves out of the web tunnel; male courtship once the female is out on the sheet, presumably to induce the female to adopt the copulatory position; and copulation. The female responded to male courtship by either sending vibratory signals through the web threads, launching an

apparent attack toward him, or adopting the copulatory position (described below). In total, the courtship behavior and copulations of *T. radiata* lasted 57 min in one pair (5 copulations) and nearly 90 min (9 copulations) in the second pair. In both cases the female eventually expelled the male from the web.

When the male walked directly toward the tunnel opening, he stopped suddenly as the female began to strum the threads of the sheet with more or less alternate movements of her palps (Fig. 1). Strumming occurred in bouts of up to 20. During a strumming movement the female first extended both palps anteriorly and then flexed first one and then the other posteriorly, snagging some threads of the sheet with the tip of the palps. These sheet threads were pulled upward (visible in some video records) until they snapped free, possibly due to the tension. The palpal movements gave the impression of scratching the sheet surface rather than twanging particular threads.

The female strumming movements apparently induced the male to stop, at least momentarily. The male then responded by rocking his body vigorously in antero-posterior direction (Fig. 2). He stood with all his legs on the sheet and shook the sheet visibly as he moved (occasionally legs I were lifted while rocking). The rocking movement was produced primarily by the antero-posterior movement of the male's body rather than by bending his legs and occurred in bouts of 3–5 rocking movements ($n = 12$). The male also frequently vibrated his abdomen once or twice just before a bout of rocking movements (5 out of 8 bouts in which illumination and angle were favorable). The female frequently stopped strumming the sheet (5 out of 7 sequences where both male and female were in focus); nearly immediately the male began to rock. If the female remained motionless after a rocking bout, the male often advanced a few millimeters toward her (2 of 8 instances). However, in most cases the female began again to strum the sheet as the male approached her, inducing him to stop and resume courtship. It seemed that in these cases the male rocked his body more vigorously before moving again toward the female that remained inside but near the tunnel opening. In one instance the female moved slowly out of the tunnel and stopped and strummed the sheet before continuing toward the male. The male rocked his body and advanced toward the female but she moved back a few millimeters and then darted at him in an attacking position (first legs slightly raised and directed forward and chelicerae spread). The male moved rapidly backward nearly 4 cm then began to rock his body again while the female returned to the tunnel.

In both pairs, after several separate bouts of rocking by the male (12 in one pair and 17 in the other), the female moved out of the tunnel, ceased strumming the sheet, and allowed the male to approach

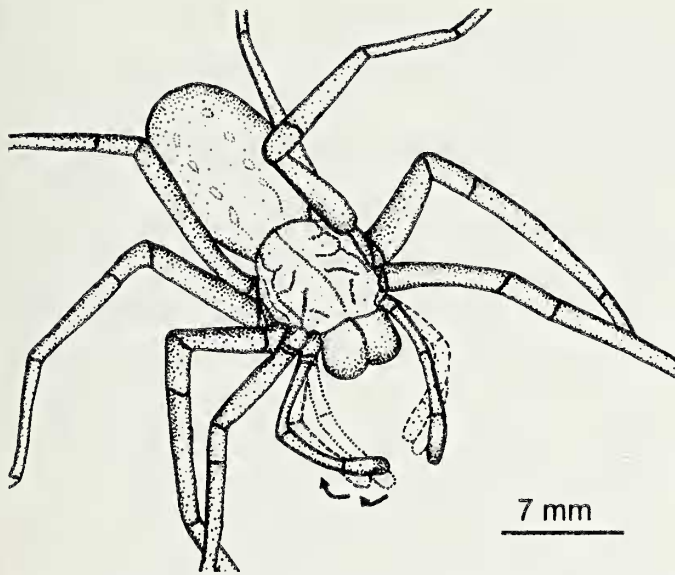


Figure 1.—Strutting movements of the female’s palps on the sheet during courtship. Arrows show the sequence of the palps’ movements: dots- initial position, dashed- subsequent position, solid-final position.

her. The male moved over the female’s body so that they faced opposite directions, and as he did so she inclined her body laterally (Fig. 3), with her epigynum exposed (copulatory position). From this position the male repeatedly contacted the female’s epigynum with one palp (Figs. 3, 4), while his other palp was held in front of his body. The male’s extended palp moved rapidly to touch the epigynum briefly and then withdrew (mean duration of extend-contact-withdraw cycle = 0.11 ± 0.02 s, $n = 37$). These movements apparently correspond to “flubs” observed in other species (Watson 1991; Stratton et al. 1996; Huber 1998; Eberhard & Huber 1998). On two occasions where the complete sequences were observed, the male made 17 and 29 flubs before the palp engaged with the epigynum and the haematodocha was finally inflated. The insertions with haematodocha expansion lasted 0.38 s (± 0.16 , $n = 5$). The haematodocha remained inflated during the entire insertion ($n = 2$). On three occasions (2 in one pair and 1 in the other, where the angle and focus were appropriate), the male was observed to move his abdomen up and down in possible copulatory courtship movements. These movements were slower than the pre-copulatory courtship vibratory

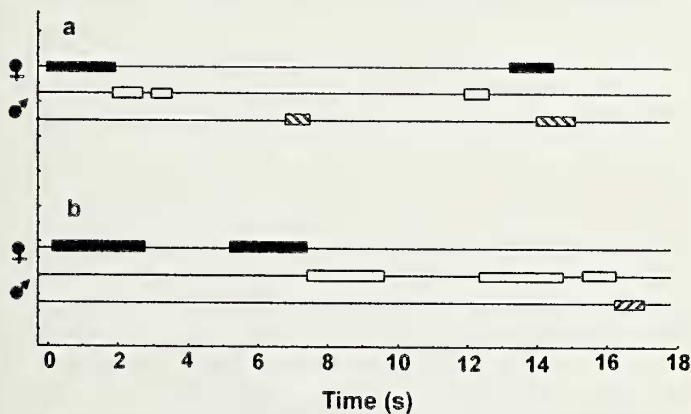
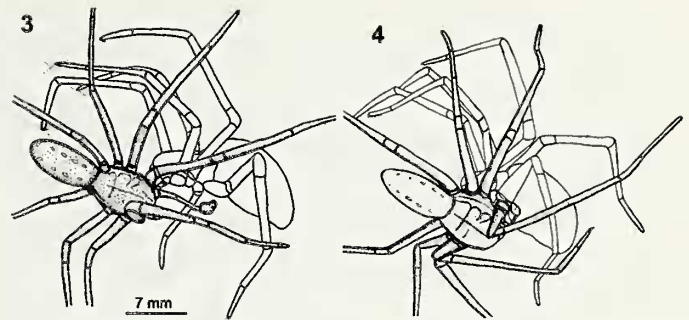


Figure 2.—Two partial sequences (a and b) of male-female courtship. Black boxes- female strutting movements, Empty boxes- male rocking movements, Dashed boxes- male moving toward the female.



Figures 3, 4.—Position of male and female previous to and during insertion. 3. The female lays on her right side as the male walks over her body. 4. Male inserting his left pedipalp (embolus) in the left opening of the female’s epigynum.

movements of the male’s abdomen, and were similar to the abdomen bobbing movement of *Leucauge* (Eberhard & Huber 1998). The pre-copulatory and copulatory courtship behaviors of a male after subsequent copulations on opposite sides were similar (e.g., flubs: 19-15-16; three subsequent copulations). The extremely short insertions were successful as one of the females produced fertile eggs. The insertions seemed to be ipsilateral (by the position of the female’s epigynum and male’s palp), although I could not be completely certain due to the dark color of the epigynum and male’s palp.

The female terminated copulation when she began to move her legs to stand on the sheet after a single successful insertion of the male’s palp ($n = 5$) or after several unsuccessful insertion attempts of the male’s palp ($n = 4$) (I could not differentiate unsuccessful insertion attempts from flubs). In one case the male remained over the female and she darted toward him in an attacking position. The female’s attack provoked an extremely rapid backward movement by the male that positioned him at 3 or 4 cm from her. After the female had ended the copulation, the male began a new approach with a sequence of pre-copulatory courtship behaviors. The courting male stopped frequently to pass his palps and sometimes his legs through his mouthparts before approaching her again; occasionally the male rubbed his palps against the sheet after grooming his palps with his chelicerae. During each new male approach, the female inclined her body toward the opposite side as the male walked over her and he immediately began to contact her epigynum with his other palp. Successive inclinations and insertions were on opposite sides ($n = 12$) except when the male failed to insert his palp in the previous attempt. In such cases the next male approach occurred on the same side of the female side that he had approached previously. The female was apparently responsible for the alternation of sides in subsequent copulations; it was clear on two occasions that she began to incline her body before the male could contact her.

Having copulated, the female did not necessarily accept the male the next time he approached her. On several occasions (10 in one pair and 4 in the other) the male stopped his approach as she began to strum the sheet, and he restarted his rocking courtship behavior. Neither male charged his palps with sperm during the courtship, indicating that males charged their palps before encountering a female.

The male’s pre-copulatory rocking and abdominal bobbing movements during copulation may reduce the female’s aggression and induce her to cooperate and use his sperm to fertilize her eggs (Eberhard 1996; Stratton et al. 1996; Eberhard & Huber 1998; Peretti et al. 2006). It is possible that these movements inform the female of the male’s quality. For example, one of the females of this study immediately lunged at and expelled from the web a small adult male (ca. 15% shorter than the males studied) that I had previously placed on her web.

The strumming behavior of the female, her ability to expel males with her attacks, and assumption of a distinctive acceptance posture, all clearly show her active role in mating (Peretti et al. 2006). This behavior possibly serves the female as a criterion for male selection as it induces the male to restart, and in some cases, seemingly to intensify his courtship behavior after he detects a female strumming. As in many other spiders, there was no indication of males being able to force females to cooperate (Huber 1996; Eberhard & Huber 1998).

It is possible to compare some aspects of the courtship behavior of *T. radiata* with that of species of other related families: Agelenidae, Lycosidae and Pisauridae (Coddington 2005). In all these families, including *T. radiata*, males mount females facing in the opposite direction (Nielsen 1932; Miller & Miller 1987; Hebets et al. 1996; Stratton et al. 1996; Huber 1998; but see Bruce & Carico 1988). However in *T. radiata* the male's courtship induces the female to incline her body to expose her epigynum, and thus his ventral surface touches (or nearly so) the ventral surface of the female, while in wolf spiders the male's ventral surface touches the dorsal surface of the female and the male's pedipalp reaches the female's epigynum around the side of her abdomen. In at least some lycosids (Stratton et al. 1996) and in several agelenids (Huber 1998) males also flub ("scrape" in Stratton et al. 1996) repeatedly prior to insertions. Copulations involve ipsilateral palpal insertion on alternating sides in all families (Stratton et al. 1996). Alternating insertions with only a single expansion of the hematodocha also occurred in *Rabidosa* spp. (Lycosinae) (Stratton et al. 1996). Female attack behavior similar to that of *T. radiata* occurs in one lycosid (Miller & Miller 1987) and one pisaurid (Arnqvist 1992). Many of these behaviors are possibly homologous with those of Tengellidae, but information about many more species is required to make stronger arguments regarding the evolution of courtship behavior in *Tengella* and related families. Particularly, the information on courtship behavior of agelenoids, the sister group of Tengellidae and lycosoids, is very important to trace the evolution of the courtship behavior in these groups of spiders.

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